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Liturgusa maya (Mantodea, Liturgusidae), the first record of an alien praying mantis in the Galápagos Islands

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Abstract

The Galápagos Archipelago, a UNESCO World Heritage site renowned for its unique biodiversity, faces increasing threats from the introduction of invasive species, particularly insects. This study documents the first record of an alien praying mantis, *Liturgusa maya* Saussure & Zehntner, 1894 (Liturgusidae), introduced to the Galápagos Islands, marking it as the second mantodean species reported from the archipelago. *Liturgusa maya* was initially detected through citizen science observations on the iNaturalist platform and taxonomically confirmed through field collections. Its presence in urban and rural areas of Santa Cruz Island since at least 2017, coupled with the apparent parthenogenetic nature of the introduced population, suggests that *L. maya* became established rapidly following a likely human-mediated introduction. A diagnosis of the species and its ootheca is provided to facilitate in-field identification, its habitat within Santa Cruz Island is delineated, and the potential ecological impacts of this introduction are explored. Additionally, the checklist of Mantodea in the Galápagos is updated, and their distribution is mapped to reflect the new findings. This discovery emphasizes the vulnerability of the Galápagos to biological invasions driven by increased human activity, highlighting the need for continued monitoring and management efforts to protect the archipelago's native and fragile ecosystems.

Keywords

Biological invasions, dispersal, endemism, island biodiversity, ootheca, parthenogenesis

Introduction

The Galápagos Archipelago, covering approximately 8000 km² and located 1000 km west of Ecuador's mainland, includes major islands such as Isabela, Santa Cruz, Fernandina, Santiago, San Cristóbal, Floreana, and Marchena, as well as smaller islands, rocks, and islets (Horwell and Oxford 2005). This volcanic archipelago, recognized as a UNESCO World Heritage site, is considered a biodiversity hotspot with significant variations in flora and fauna across each island (Jackson 1993, Harpp et al. 2014). Although the Galápagos Islands are primarily known for their iconic vertebrate fauna, such as giant tortoises, marine iguanas, and Darwin's finches, and their unique adaptations (von May 2021, Kricher and Loughlin 2022), the Archipelago is also home to an important diversity of native and endemic insects (Linsley and Usinger 1996, Peck 2001).

The insect fauna of the Galápagos has evolved various adaptations to the archipelago's peculiar geographical and climatic conditions, playing a fundamental role in local ecosystem functioning (Peck 2001). However, introduced species, particularly arthropods, now represent a significant threat to the Galápagos ecosystem, with 562 of the 651 introduced species (86.33%) being insects (Charles Darwin Foundation 2024). These alien species often compete with local fauna for resources, may introduce new diseases, and can lead to cascading ecological effects (Simberloff et al. 2013). This impact is particularly concerning in the Galápagos archipelago, where species have evolved in relative isolation and may lack the necessary defenses to cope with invaders (Vitousek 1998, Blackburn et al. 2014). Some introduced insect species already score high in their invasiveness impact, causing significant disturbances to local biodiversity and human residents (Roque-Albelo and Causton 1999). Examples include the paper wasps *Polistes versicolor* (Olivier, 1792) and *Brachygastra lecheguana* (Latreille, 1824), the ants *Solenopsis geminata* (Fabricius, 1804) and *Wasmannia auropunctata* (Roger, 1863), and the cottony cushion scale *Icerya purchasi* (Maskell, 1878), among others (Causton et al. 2006). Because invasive species pose the most significant threat to the biodiversity of the Galápagos Islands (Causton et al. 2006, Sampedro et al. 2020), documenting newly established species is a critical first step in assessing their potential for invasiveness and formulating management strategies.

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The objective of this study was to formally report the discovery of a newly introduced species in the Galápagos, *Liturgusa maya* Saussure & Zehntner, 1894, a praying mantis recently reported in the archipelago through observations made by citizen scientists on the iNaturalist platform. We provide a diagnosis of this species and its ootheca to facilitate field recognition and to discuss the adaptations that may have facilitated its arrival and establishment in the Galápagos and its potential ecological impact. Additionally, we take this opportunity to update the checklist of Mantodea in the Galápagos and map their distribution.

Materials and methods

To investigate the likely colonization timeline of *Liturgusa maya* in the Galápagos Islands, we employed a combination of observational records by CDF staff, the citizen science platform iNaturalist, and field collections. Taxonomic identification was confirmed through the treatment of *Liturgusa* by Svenson (2014a).

To map the distribution of *L. maya* across both its introduced and native ranges, we extracted georeferenced data from iNaturalist and literature records as data points and used QGIS 3.38.0 to create a distribution map. For country boundaries, we used freely available data from Natural Earth. We utilized the shapefile 'isla_a' for island boundaries, obtained from topographic maps on the Geoportal of the Military Geographical Institute of Ecuador. All layers were processed in QGIS using the WGS84 projection.

Results

Recognition and diagnosis of L. maya *(Figs 1A–E, 2A, B).*—Body flattened and relatively narrow, with thick mid- and hind-femora but thin tibiae. Body length ranges from 24 to 34 mm in females and 19 to 25.5 mm in males, with the latter being slightly smaller and slimmer overall (Svenson 2014a). The body and forewing background color varies from pale green to yellowish-green, with a strong mottling of light to dark brown, and dark-banded legs. Most individuals exhibit a distinct forewing patterning consisting of the following two features: i) a relatively large pre-medial blotch (characterized by a region where both veins and membranes are predominantly pale) that is often fully or partially surrounded by dark-colored membranes and pale crossveins, and ii) longitudinal veins posterior to the pre-medial blotch that are predominantly pale but interrupted by unequally spaced, darkened sections. Some individuals display asymmetrical forewing coloration, with one wing mottled and the other markedly darkened, sometimes with a reddish tone. The darker wing is usually tucked under the typically colored wing. In the resting position, the wings cover most of the abdomen, sometimes reaching its tip. Hindwings are darkened, their posterior half is slightly translucent, and their anterior margin is narrowly delineated in a reddish tone.

The ootheca is shaped like a round-bottom bottle (Fig. 2A). The external wall is caramel brown, thick, and smooth. The

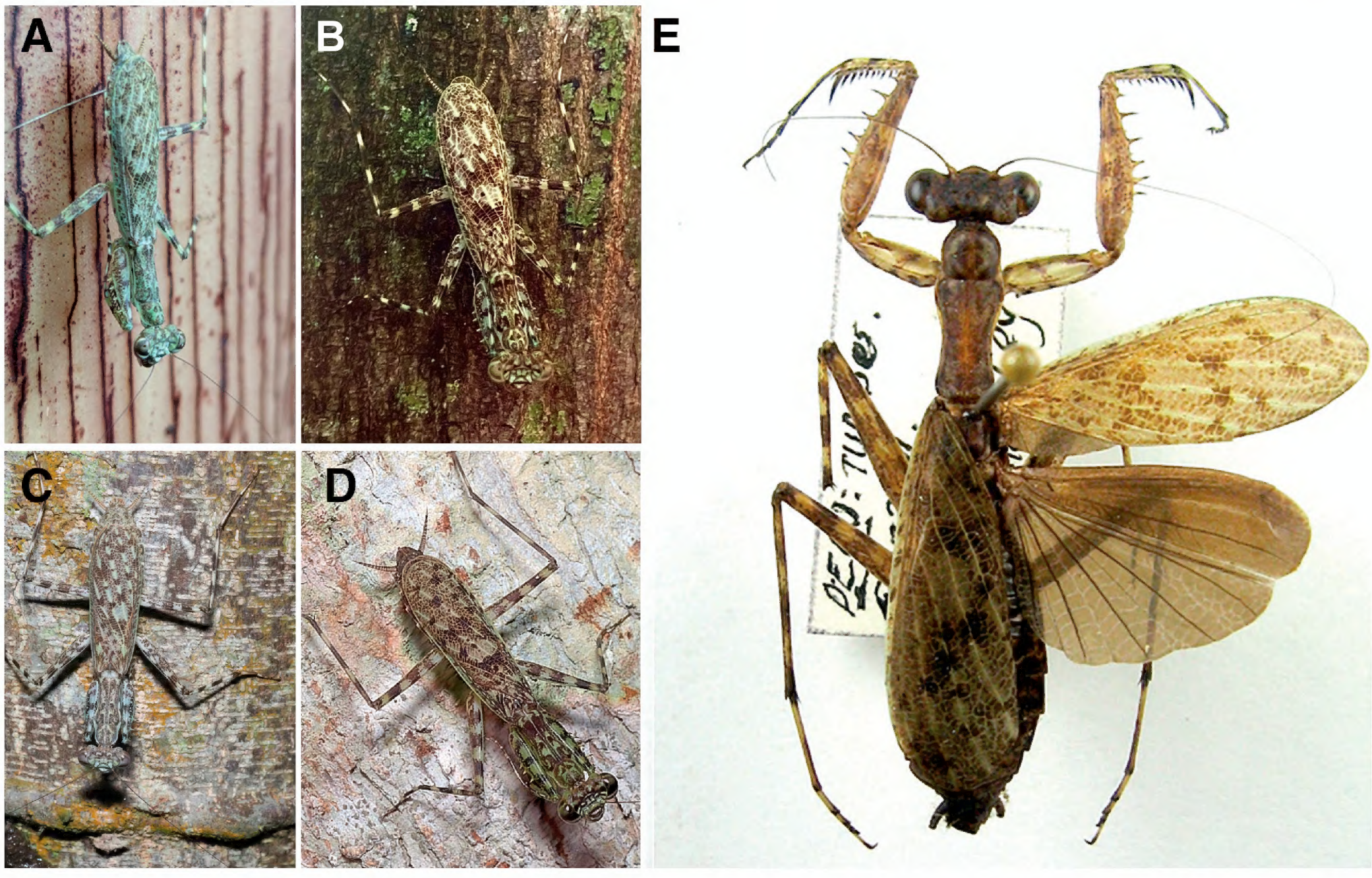

Fig. 1. *Liturgusa maya*, habitus of adult specimens. **A.** Female observed in Bellavista, Santa Cruz, Galápagos Islands (iNat Obs: 196999892; photo by Zihao Wang, License CC-BY); **B.** Female observed in Orange Walk, Belize (iNat Obs: 167452365; photo by Claire Ayer, License CC-BY-NC); **C.** Male observed in Jalisco, Mexico (iNat Obs: 232941914; photo by Barry Sullende, License CC-BY-NC); **D.** Male observed in Huánuco, Peru (iNat Obs: 44474645; photo by Dieter Schulten, License CC-BY); **E.** Female from Tumbes, Peru. All iNat images were cropped from the original to enhance visualization.

ootheca abruptly tapers into a rigid, short tubular projection of a much darker brown tone, at whose tip a single emergence opening can be observed. Females attach their egg cases to flat substrates, such as bark, by their proximal end so that the tubular projection always points upward.

Specimens examined.—ECUADOR, Galápagos Islands • 1 ♀; Santa Cruz Island, Charles Darwin Foundation; [-0.742244, -90.304161]; 1/IX/2023; L. Betancourt leg.; manual collection; ICCDRS 52235 • 1 ♀; Santa Cruz Island, El Cascajo; [-0.669192, -90.271656]; 3/IV/2023; J. Ramírez leg.; manual collection; ICCDRS 52233 • 1 ♀; Santa Cruz Island, El Cascajo; [-0.669192, -90.271656]; 23/VIII/2023; J. Ramírez leg.; manual collection; ICCDRS 52234 • 1 ♀; Santa Cruz Island, Bellavista; [-0.69345, -90.32244; 18/XII/2023; P. Picón and J. Avendaño leg.; manual collection; ICCDRS 53348 • 1 ♀; Santa Cruz Island, Bellavista; -0.69345, -90.32244; 18/XII/2023; P. Picón and J. Avendaño leg.; manual collection; ICCDRS 53349 • 1 ♀; Santa Cruz Island, Bellavista; -0.69345, -90.32244; 18/XII/2023; P. Picón and J. Avendaño leg.; manual collection; ICCDRS 53350 • 1 ♀; Santa Cruz Island, Bellavista; -0.69345, -90.32244; 18/XII/2023; P. Picón and J. Avendaño leg.; manual collection; ICCDRS 53351.

iNaturalist and literature records (introduced and native ranges).—See Suppl. material 1.

Observational records.—Puerto Ayora, XII//2018 (P. Picón obs.) [ICCDRS 17281]; 1 juvenile, El Cascajo, 19/ XI /2021 (L. Betancourt obs.) [ICCDRS 17282].

Geographic distribution and habitat preferences.—*Liturgusa maya* inhabits the tropical and northern subtropical regions of the American continent (Fig. 3). Specifically, *L. maya* is distributed from southern Mexico through Central America into northwestern South America (Colombia, Venezuela, Ecuador, and northernmost Peru) and western Amazonia, extending as far south as southwestern Peru (Svenson 2014a). As such, *L. maya* is one of the few trans-Andean praying mantises in the neotropics (Rivera and Vergara-Cobian 2017). Outside its native range, an introduced population of *L. maya* is established in Florida (Nisip et al. 2019). *Liturgusa maya* uses the vertical surfaces of tree trunks as hunting grounds, predominantly favoring medium-sized, smooth-bark tree trunks in forested areas. They are shy insects capable of running up and down tree trunks and other vertical surfaces with uncanny agility, making collection difficult. Additional bionomics of *L. maya* can be found in Anderson (2018) and Castillo-Carrillo et al. (2022).

Updated checklist of the praying mantises of Galápagos.—The following checklist follows the taxonomic classification proposed by Rivera and Svenson (2016, 2020); it incorporates the concept of the superfamily Thespoidea, as outlined by Schwarz and Roy (2019), to provide a more comprehensive systematic framework.

Fig. 2. A. Oothecae of *L. maya* (two different specimens from La Maná, Ecuador; photos by Hiromi Yagui); **B.** Juvenile specimen of *L. maya* on tree bark near the agriculture zone El Cascajo (photo by Lenyn Betancourt, 19-NOV-2021).

Taxonomy

ORDER MANTODEA Latreille, 1802
Superfamily Thespoidea Saussure, 1869
Family Thespidae Saussure, 1869
Subfamily Thespinae Saussure, 1869
Tribe Thespini Saussure, 1869
Genus *Galapagia* Scudder, 1893

***Galapagia solitaria* Scudder, 1893**

Distribution in Galápagos.—Baltra, Española, Fernandina, Floreana, Genovesa, Isabela, San Cristóbal, Santa Cruz, Santa Fé, Santiago, and Seymour Islands.

Habitat.—Ground level and herbaceous plants, ranging from arid to humid forest environments.

Remarks.—This species shows considerable variation in size, body proportions, and coloration throughout its range. Male genitalia, however, exhibit little variation. Although the entire Galápagos population is treated as one species, genetic studies will be necessary to reassess its taxonomic status and unveil its evolutionary history and dispersal patterns across the archipelago.

Relevant references.—Peck (2001), Svenson (2014b), Rivera and Vergara-Cobián (2017), Rivera and Svenson (2020).

Superfamily Acanthopoidea Burmeister, 1838
Family Liturgusidae Giglio-Tos, 1915
Subfamily Liturgusinae Giglio-Tos, 1915
Tribe Liturgusini Giglio-Tos, 1915
Genus *Liturgusa* Saussure, 1869

***Liturgusa maya* Saussure & Zehntner, 1894**

Distribution in Galápagos.—Santa Cruz and Santiago(?) Islands.

Habitat.—Tree trunks and human-made vertical structures in rural and urban areas.

Relevant references.—Svenson (2014a), Anderson (2018), Nisip et al. (2019), Castillo-Carrillo et al. (2022).

Discussion

Mantodea was first reported in the Galápagos Islands with the description of *Galapagia solitaria* Scudder, 1893 (Thespidae), endemic and widespread in the Archipelago (Fig. 3). Until the present report, *G. solitaria* was the only praying mantis known in the archipelago (Hebard 1920, Peck 1996, 2001, Rivera and Vergara-Cobián 2017, Rivera and Svenson 2020). The Galápagos Islands have a rich history of insect surveying, and both native and introduced fauna are relatively well-known for some groups (e.g., Linsley and Usinger 1966, Peck 2001). Therefore, we consider it unlikely that *L. maya* escaped detection during the various insect surveys conducted on the islands. The absence of references to bark mantises in the Galápagos in the historical literature, their sudden emergence on iNaturalist, and their association with buildings and trees near urban centers and agricultural lands suggest that it is a recent arrival to the Archipelago (Peck et al. 1998).

The first observational record of *L. maya* on the Galápagos Islands (Santa Cruz) dates back to July 2018 (ICCDRS Observation 17281). Since no taxonomic identification was attempted, this early observation remained unpublished. The first confirmed public photographic record of *L. maya* on iNaturalist, an adult female observed on tree bark at the edge of agricultural lands north of Puerto Ayora (Santa Cruz Island), dates back to February 10, 2020. A juvenile specimen, presumably of this species, was spotted in the same general area and photographed by LB (ICCDRS 17282) in 2021. iNaturalist also includes another record from 2021, an early-instar nymph of a bark mantis from Santiago Island (https://www.inaturalist.org/observations/868754780); however, we could not corroborate its presence there with collected specimens or its taxonomic identity. Subsequent sightings of adults and nymphs on Santa Cruz Island are documented from 2023 and 2024 on iNaturalist, including observations in more urbanized zones. All adult specimens on iNaturalist are females and temporarily overlap with nymphs. They have been observed on walls near or inside buildings and on tree bark near agricultural lands. Given the current evidence and considering developmental times, we estimate that *L. maya* has been present on Santa Cruz Island continuously since at least 2017.

The means of introduction and the number of colonization events are unknown. The unintentional introduction of exotic insects due to the rising volumes of imported food and construction materials from the mainland is an ongoing concern to local authorities. Approximately 75% of the agricultural food supply was transported from the mainland in 2017 to supply both the booming tourist industry and the local population, and is projected to grow to up to 95% by 2037 (Sampedro et al. 2020). It is therefore reasonable to assume that *L. maya* arrived in the Galápagos among agricultural products or construction materials, all of which provide safe traveling conditions for stowaway individuals. The same can be said of the oothecae, which resemble a piece of bark or organic debris (Svenson 2014a, Rivera and Svenson 2016, Nisip et al. 2019) and can easily go unnoticed by untrained eyes during inspections. The arrival of *L. maya* in the Galápagos underscores a broader trend identified by Peck et al. (1998): As the human population on the islands grows, so does insect diversity.

Different factors determine the likelihood of invasiveness in insect species. Effective dispersal mechanisms play a pivotal role in facilitating rapid and widespread colonization. The association with human activities further enhances the success of invaders, benefitting from multiple avenues for introduction and spread across altered landscapes, agricultural settings, and global trading networks (Perings et al. 2000). Upon arrival, broad environmental tolerance and dietary preferences enable invaders to exploit diverse food sources under various ecological conditions, and the absence of natural enemies (predators, parasites) allows for unchecked population growth, further contributing to their widespread establishment. Once settled, the introduced species may outcompete and displace local ones and, under the right conditions, they may incur significant ecological and economic expenses, with costs persisting and increasing in the long run (Levine and D'Antonio 2003). Therefore, successful invasions result from a complex interplay of biological traits and ecological adaptations.

Indeed, *L. maya* possesses all the hallmarks of a successful colonizer. It is widely distributed and one of the most widespread

praying mantis species in the Neotropics (Fig. 3). The species occupies diverse environments across its range, including both tropical and seasonally dry forests (Svenson 2014a, Juárez-Noé and González-Coronado 2020). Besides its occurrence in forest habitats, *L. maya* is well-adapted to human-altered landscapes (e.g., parks and semi-urban areas) where it can be found on various artificial structures analogous to their natural tree-based habitats, such as poles, fences, and wooden constructions (JR, personal observation). Notably, *L. maya* has also been found to be associated with tree crops, including cacao (Castillo-Carrillo et al. 2022). The broad range of environmental preferences is also likely linked to a generalistic diet, enabling these mantises to take advantage of local resources more effectively. Oothecae attributes, including their hardiness, cryptic appearance, and high egg capacity, protect developing embryos from environmental stressors, significantly aiding the spread of *L. maya* in non-native ecosystems. Moreover, *L. maya* is known to exhibit facultative parthenogenesis, allowing it to establish a population through asexual reproduction, as is believed to have been the case for the introduced population uncovered in Florida (Anderson 2018). The ability of certain insect species to reproduce asexually enhances their probability of colonization, offering reproductive flexibility, optimal resource utilization, and swift population expansion (Caron et al. 2014). All these factors combined have likely contributed to the arrival and establishment of *L. maya* in its novel environments.

Local impacts.—Evaluating the effects of introduced species, particularly in the early stages of colonization, is inherently challenging. With the recent introduction of *L. maya*, it is still too early to estimate its impact. However, the species' distinct life history traits provide a basis for hypothesizing potential interactions and effects.

Liturgusa maya is a generalist predator inhabiting tree bark, so its influence is likely confined to arthropod communities within these environments. In the disturbed agricultural zones of Santa Cruz Island, *L. maya* is more likely to interact with other introduced species, as these comprise more than 80% of arthropod diversity in such environments (Wauters et al. 2017). Therefore, the species composition of arthropod communities in the habitat of *L. maya* on Santa Cruz Island may mitigate its impact on the local endemic arthropod fauna. *L. maya* is also likely to interact with ants, which are diverse and abundant in the agricultural zones of Santa Cruz Island (Herrera et al. 2020). However, ants are common in the natural habitat of *L. maya*, suggesting that it is likely preadapted to either avoid or utilize ants as a food source. The introduced species *Solenopsis geminata*, which is abundant in the habitat of *L. maya* in the Galápagos, is known to significantly impact other arthropods (Wauters et al. 2017) and could represent a limiting factor to the establishment and future spread of *L. maya*.

Liturgusa maya may engage in intraguild competition with other bark-dwelling predators, such as the spider *Selenops mexicanus* Keyserling (Selenopidae) (Fig. 4A, B), which has also been introduced to the Galápagos and is recorded on multiple islands (Crews et al. 2016). Both species employ similar bark-hunting tactics, including flattened bodies with disruptive coloration and swift movements around tree trunks for hunting and evading danger (Fig. 4A, B). Since both species are sympatric on Santa Cruz Island and occupy similar ecological niches, competition between them could affect their local population dynamics, influencing their distribution and abundance within the shared habitat. Conversely, *L. maya* is unlikely to compete with the other praying mantis species in the archipelago, *G. solitaria*. As a member of Thespini, *G. solitaria* hunts

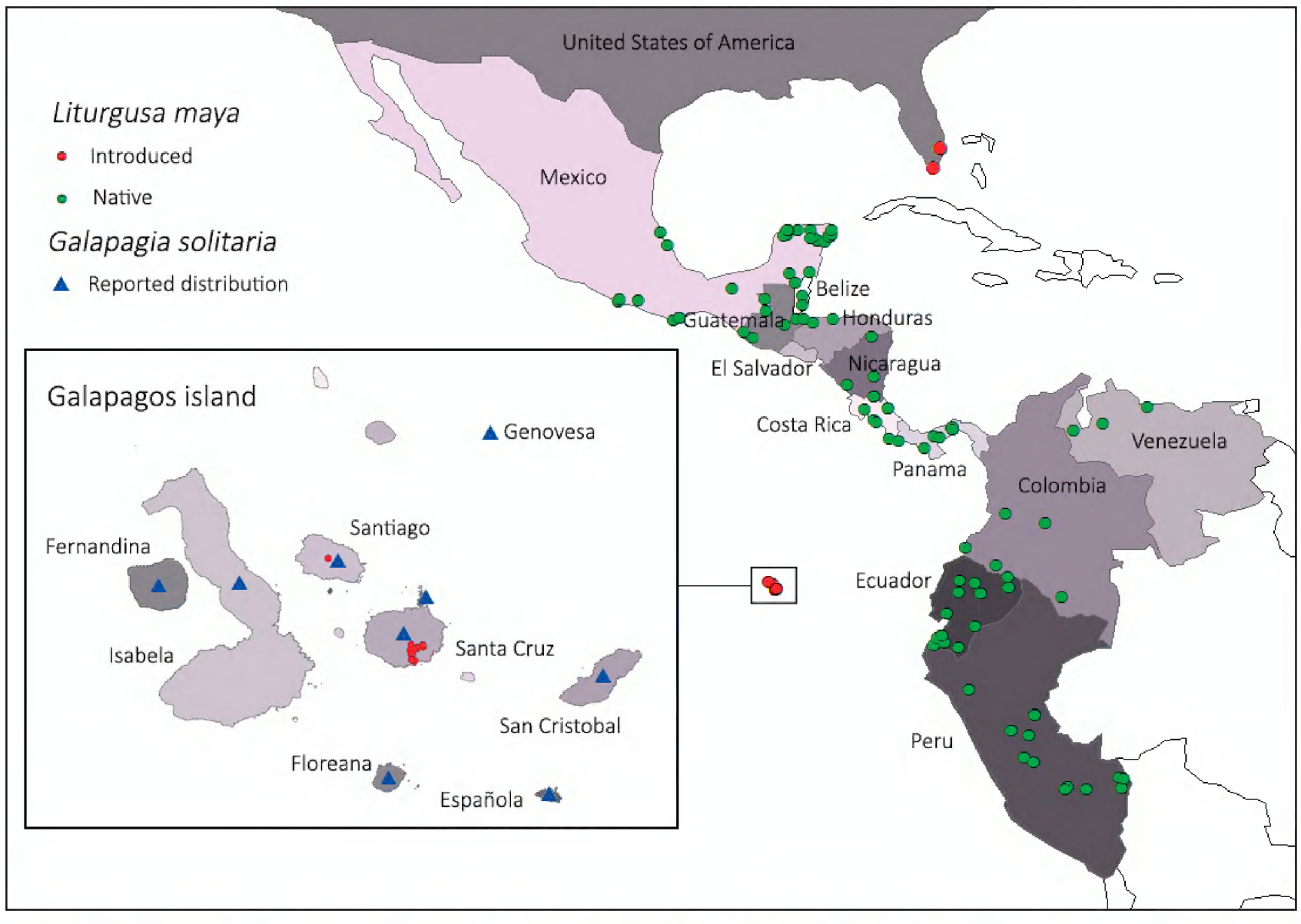

Fig. 3. Geographic distribution of *L. maya* (native and introduced ranges; data in Suppl. material 1 and *G. solitaria* (presence only).

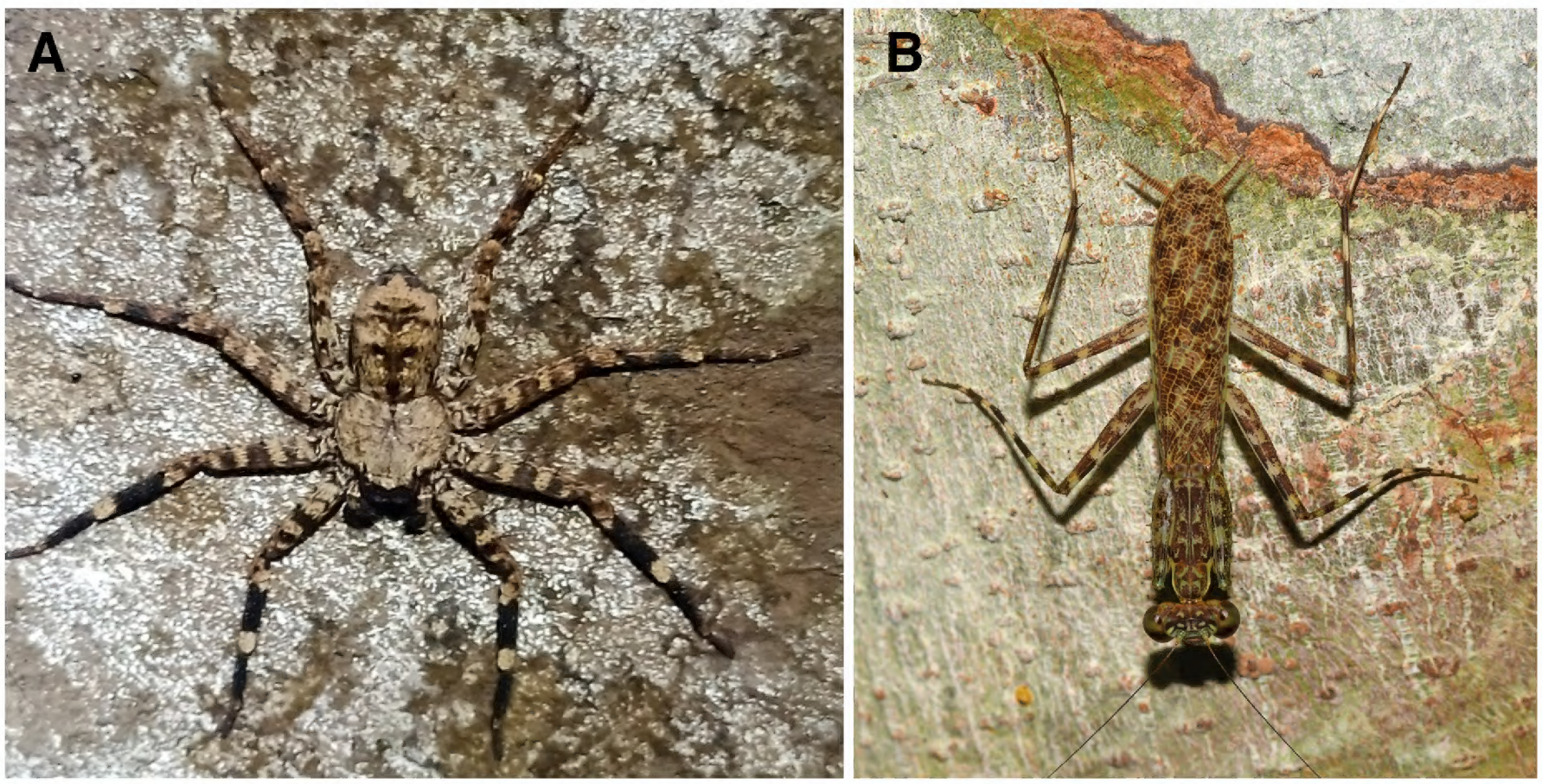

Fig. 4. A. *Selenops mexicanus* from Galápagos Islands (iNat Obs: 156509948; photo by Carlo Catoni, License CC BY-NC); **B.** *L. maya* (male) from Peru (iNat Obs: 195977594, photo by Josh Vandermeulen, License CC BY-NC-ND). All images were cropped from the original for enhanced visualization.

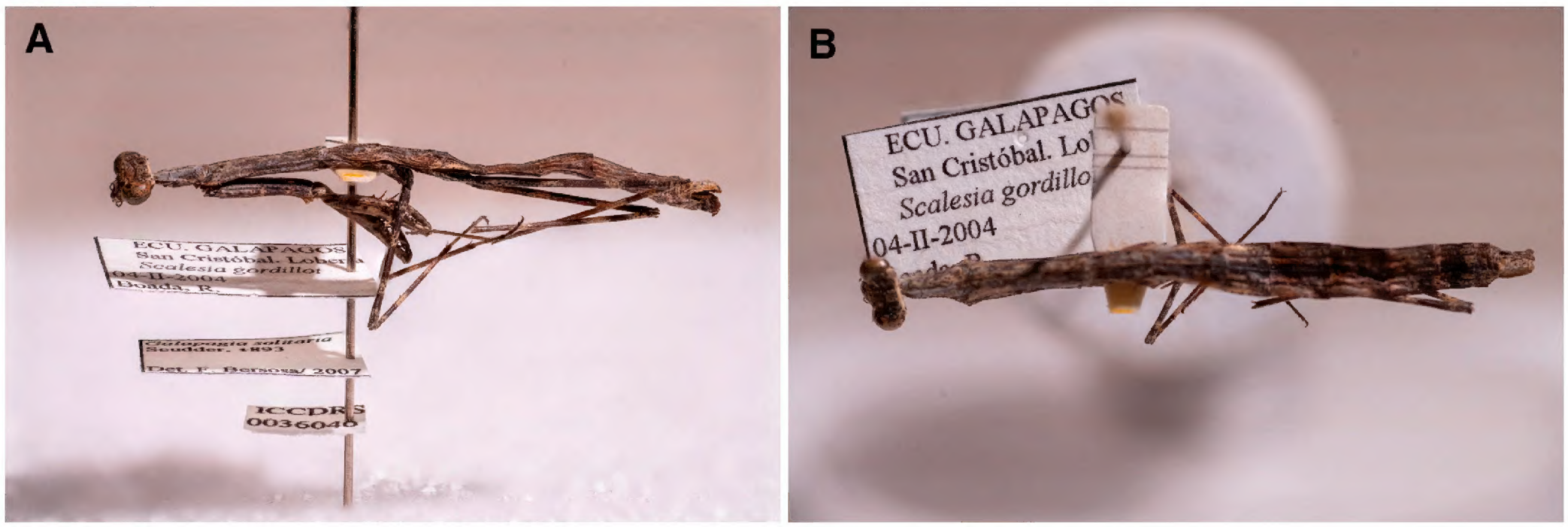

Fig. 5. The Galápagos endemic *Galapagia solitaria*, female specimen from San Cristóbal Island. **A.** Lateral view; **B.** Dorsal view. Photo by Carlos Espinosa/CDF, 24-SEP-2022.

at ground level and on low vegetation, where its characteristic stick-like appearance (Fig. 5A, B) and discreet gait provide effective camouflage. Given that *L. maya* and *G. solitaria* occupy different niches, direct interaction or displacement is unlikely.

Although it is too early to draw definitive conclusions about the ecological impacts of *L. maya*, its role within the Galápagos arthropod communities will likely depend on its interactions with both native and introduced species. The species' adaptability and its tendency to occupy bark-dwelling habitats suggest that it could integrate into the existing ecosystem in a way that may not lead to direct displacement of native species but rather may coexist with or exploit available resources. Additionally, *L. maya*'s predatory behavior, particularly in urban and rural environments, could contribute to reducing populations of insects that move along tree trunks and human-made vertical structures, potentially providing pest control services. Further monitoring of *L. maya*'s distribution and interactions will be essential to understanding its long-term impact on local biodiversity and its potential as a natural pest control agent.

Conclusions

Liturgusa maya is the first species of praying mantis recorded as introduced in the Galápagos Islands and the second species of Mantodea identified in the archipelago. Its presence near Puerto Ayora on Santa Cruz Island was initially detected through observations by citizen scientists on iNaturalist and confirmed with museum specimens. The species is found in both urban and rural areas on Santa Cruz Island. The information collected suggests that *L. maya* has been present on the island since at least 2017, possibly earlier, with its arrival likely facilitated by human transport. To date, only females have been observed, indicating that facultative parthenogenesis may have played a significant role in its establishment and spread in Santa Cruz. This report represents the second known introduced range for *L. maya* after Florida and its first insular record, adding to the growing global list of introduced praying mantis species documented over the past decade.

Follow-up studies examining the genetic diversity in this introduced population will be key to uncovering its most likely geographic source and determining whether its presence in the Galápagos resulted from one or multiple colonization events. This information will provide a baseline for exploring genetic variation within the population, which is crucial for understanding its adaptability and potential impact on local ecosystems. Additionally, it will offer valuable insights into the mechanisms underlying the initial stages of colonization of alien praying mantises.

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Supplementary material 1

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Data type: xlsx

Explanation note: Occurrence data for *Liturgusa maya*, illustrating its known range across both native and introduced regions. This data was used for the elaboration of the map in Fig. 3.

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